SPOLIA RUNIANA.—III. The Distribution of certain Diatoms and Copepoda, throughout the year, in the Irish Sea.

By W. A. HERDMAN, F.R.S., F.L.S., Professor of Zoology in the University of Liverpool.

(With 21 Text-figures.)

[Read 1st November, 1917.]

Reprinted from Journ. Linn. Soc., Bot. vol. xliv. (1918), pp. 173–204.

PART of the work * of the yacht 'Runa' for some years previous to 1914 consisted in taking periodic samples of the marine plankton at various localities around Port Erin, at the south end of the Isle of Man, during the two most interesting times in the annual cycle—viz., spring (March–April) and autumn (July–September). During the remaining months, when the yacht was not in commission, plankton gatherings in Port Erin bay were taken with great regularity at the rate of six in the week, three at a time on two occasions per week, two of the three hauls being horizontal and the third vertical. This systematic plankton survey has been continued for fully 10 years (1907–1917 inclusive), and over 5000 † samples have been collected and examined. The general results of this intensive study of the plankton of a central area of the Irish Sea have been given in a series of reports ‡ drawn up in collaboration with Mr. Andrew Scott, A.L.S., and others, and published by the Lancashire and Western Sea-Fisheries Committee; but the material and statistics collected still contain much information which has not yet been made use of. It is proposed in the present communication § to deal with the records of the occurrence throughout the year in our district of a few of the most abundant of the Diatoms and the Copepoda which make up the bulk of the phytoplankton and of the zooplankton respectively at those periods of the year when they are most abundant. At the time of the spring maximum (usually in April or May) a small silk tow-net hauled for about 15 minutes through about half-a-mile of the surface water of the Irish Sea will usually catch some millions of individual Diatoms (up to a couple of hundred millions ‖ on occasions), constituting probably, on the average, some 999,999 out of each million of organisms in the gathering ¶. This is almost

---

[*] For Parts I. and II. of "Spolia Runiana" see Journ. Linn. Soc., Zool. xxxii. p. 163 (1913), and p. 269 (1914).

[†] More precisely 5116, to the end of 1916.

[‡] Trans. Biol. Soc. Liverpool, xxii. (1908) to xxxi. (1917).

[§] I wish to acknowledge, with thanks, the help I have received in the preparation of these plankton records from Mr. Andrew Scott, A.L.S., and from my secretary, Miss H. M. Lewis, B.A. Mr. Scott took for me the excellent photo-micrographs of the plankton from which most of the illustrations have been reproduced.

[‖] Estimated by counting measured samples.

[¶] The average of a number of cases where smaller, but still very large, hauls of Diatoms were taken is—Diatoms=about 99 per cent. of the total organisms present.

a pure sample of Diatoms—a "monotonic phytoplankton." Similarly, when the zooplankton is at its height in late summer (usually September) the same net may contain almost a pure gathering of Copepoda numbering some tens to hundreds of thousands of individuals (up to 214,000), and making up perhaps 999 out of every thousand organisms present—a "monotonic zooplankton." But we may still regard the gathering as a zooplankton if over 50 per cent. of the organisms are animals—on account of their greater bulk.

Moreover, these very abundant Diatoms and Copepoda belong in each case to very few species, so that one can select about half-a-dozen species of Copepoda which constitute by far the greater part of the summer zooplankton, and about the same number of Diatoms which similarly make up the bulk of the spring phytoplankton. These few species, belonging to these two very widely separated groups, thus come to be the most significant organisms in relation to the annual metabolic cycle of our seas and the food-supply from our coastal fisheries. Consequently it is of both scientific and economic importance to obtain such data as seem possible from our long series of observations, extending over a decade, as to the occurrence of these dominant factors in the plankton. No doubt there are exceptional years with unusual occurrences which will have a disturbing effect, but the ten or eleven years' results ought to give us an average of some value.

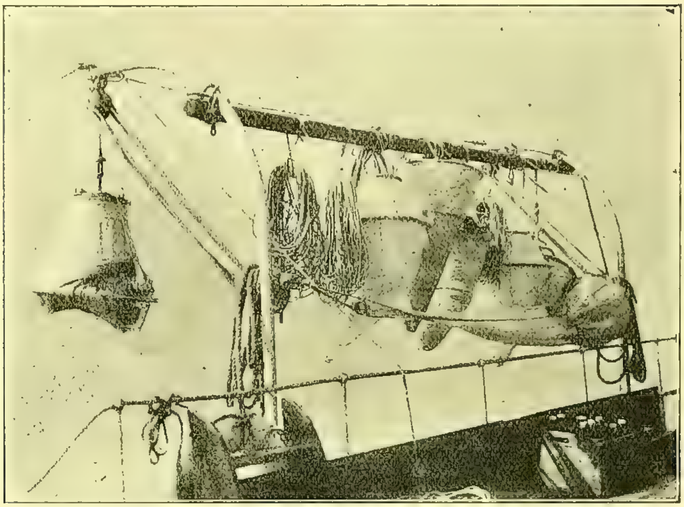

FIG. 1.—"Hensen," "Nansen," "Funnel" and other plankton nets drying after use on the yacht.

We have endeavoured, in our work from the yacht, as the result of many experiments, to make use of a standard net in a constant manner so that the hauls should be approximately comparable. Our two horizontal tow-nets of fine-meshed miller's silk (No. 20 and No. 9) measure 35 cm. (about 14 inches) in diameter at the mouth, and are in our weekly gatherings throughout the year hauled through a definite course in the open water of Port Erin bay. The two together ("coarse" and "fine" nets) constitute a "standard haul." The gatherings taken outside the bay during the periods of the vernal and autumnal plankton maxima were made with the same nets as in the bay, at fixed "stations" respectively three and five (and on a few occasions ten) miles from land *.

In addition to these standard hauls many others were taken with special nets, such as the closing "Petersen-Hensen" and "Nansen," the "shear-net" and "funnel-nets," usually at depths of 5 to 30 fathoms, and on occasions down to 60 fathoms out in the deep central valley between the Isle of Man and Ireland. Figure 1 gives a general view of the various nets used on one of our plankton cruises. Temperatures, surface and deeper, weather observations and water-samples were also taken systematically †.

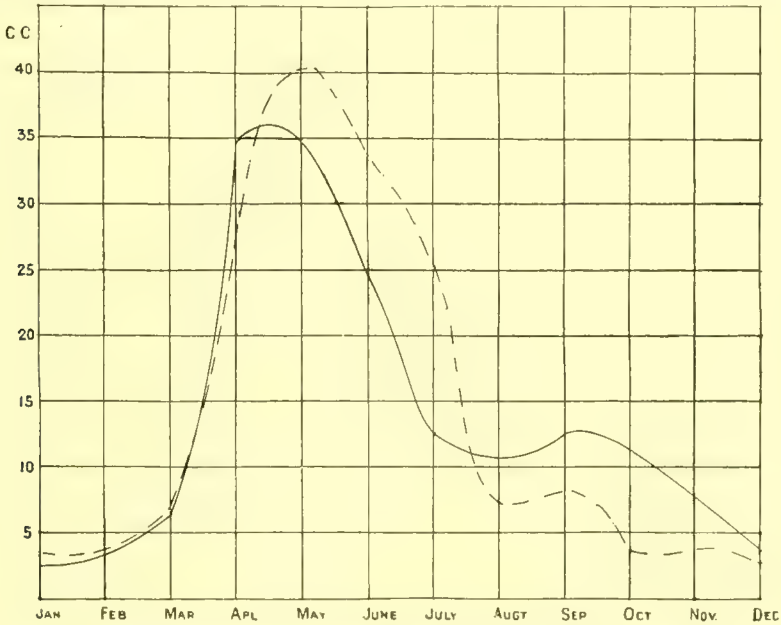

FIG. 2.—Typical Irish Sea plankton curves for the years 1913 (dotted line) and 1914 (whole line).

The plankton gatherings when taken are at once treated with formol to kill and fix the organisms and prevent further changes. They are then placed (at the Port Erin Biological Station) in graduated cylinders, and after some hours, when the material has fallen to the bottom and the superjacent fluid is clear, the quantity of plankton in cubic centimetres is recorded. The fixed plankton is then concentrated and preserved in

---

* Determined by cross-bearings, and by distance run calculated from the engines.

† For further particulars as to methods, see the earlier reports published by the Lancashire and Western Sea-Fisheries Committee.

5 per cent. formol, and is re-measured it may be weeks later when submitted to detailed examination. It is this last more accurate measurement that has been made use of for calculations and curves. The first estimation of the volume is only taken in case some accident happens later; but we have been very fortunate in that respect: we have only lost about 10 gatherings in the 10 years out of over 5000 samples. Figure 2 shows typical plankton curves for the years 1913 (dotted line) and 1914, taken from the recorded monthly averages of the plankton hauls. As an example of the height to which individual hauls may rise in spring, I may quote from our records of this year that on April 18th, 1917, the standard haul measured 165 c.c., and on April 19th 150 c.c., and consisted mainly of *Chætoceras*.

Our confidence that these samples are adequate and representative receives support from the fact that the same organisms are recorded in much the same quantities year after year, and that practically no new forms turn up. Mr. Andrew Scott, A.L.S., who has made a detailed microscopic examination of all the material for the purpose of determining the species, has met with none new to science. Some rare species previously unknown in British seas, such as the Norwegian Copepod *Microcalanus pusillus*, Sars, which appeared first in our deeper nets in the summer of 1907, and the Indo-Pacific Diatom *Biddulphia sinensis*, Grev., have occurred; but throughout the series of over 5000 gatherings, extending over nearly every week of 10 years, no species actually new to science has been determined from the macroplankton. The various new Copepoda which have been described from time to time from our work at Port Erin have all been bottom-living forms obtained by dredging. This is, so far, a satisfactory result of our work, as it seems to indicate that probably all the pelagic species of Copepoda in our sea are now known. It is not the rare species that are of most interest. They may have an interest of their own—morphological or distributional—but for my present purpose it is the common species that are of most importance, those species which by their abundance in nature play their part in providing fish-food for man or in affecting the public health either by keeping the sea clean or by causing plagues.

For the purpose then of arriving at some conclusion as to the distribution throughout the year of these really significant organisms, I have picked out from our records the following six species of Copepoda as being undoubtedly the most abundant and economically the most important representatives of that section of the plankton:—*Oithona helgolandica* (= *similis*), *Pseudocalanus elongatus*, *Acartia clausi*, *Temora longicornis*, *Paracalanus parvus*, and *Calanus finmarchicus*. These are all cases of genera where there is only one species in our seas (e. g., *Calanus*) or only one common species (e. g., *Oithona*), so that we are dealing with half-a-dozen very distinct forms, and there can be no doubt as to what is in question even if the genus only is referred to.

When we turn to the Diatoms the case is rather different. There several of the more prominent genera are represented by a number of common species, and moreover some of the species are closely related, and variable, so that doubts may arise as to the exact identifications, and authorities may differ as to the relative proportions in which certain species or varieties of, say, *Chætoceras* or *Biddulphia* are present in the plankton. Under these circumstances I have considered it will best serve my purpose, which is a general and economic rather than a detailed speciographic one, if I deal with generic titles only, grouping together for example all the species of *Chætoceras* that may occur under that one name. I have chosen the following genera as being the most important representatives of the Diatoms in our plankton :—*Biddulphia*, *Chætoceras*, *Coscinodiscus*, *Rhizosolenia*, *Thalassiosira*, *Guinardia*, and *Lauderia*. In some of these genera (e. g., *Guinardia* and *Lauderia*) as in the case of the Copepoda there is only one possible species in question, in *Biddulphia* it is in most cases only the species *B. mobiliensis*, but in others (e. g., *Chætoceras, Coscinodiscus*, and *Rhizosolenia*) there are usually several allied species occurring together in profusion in any large gathering of the genus.

I may add that our commonest species in the Irish Sea off Port Erin are not necessarily those that are most abundant in other seas of North-West Europe. For example, in the Baltic near Kiel, according to Lohmann, the most abundant Diatom is *Skeletonema costatum*, a comparatively rare form in our plankton, and George Murray similarly found that to be the commonest form he had met with in a plankton survey of some of the more sheltered lochs of the West of Scotland. It is, however, one of the minuter forms which readily escapes notice, and may to a considerable extent pass through the meshes of the net.

Then again, in July 1911, in Upper Loch Torridon, on the West Coast of Scotland, I got a haul of 334,000,000 *Nitzschia delicatissima*, which is rare with us in the Irish Sea, but is apparently more abundant at Plymouth.

I think it probable, however, that our Port Erin results will be found to hold good for the more open sea-water of high salinity * around the British Isles. A valuable paper which appeared recently on the Plankton of Plymouth Sound, by Dr. Marie V. Lebour †, while dealing mainly with the more minute Protozoa and Protophyta which escape the tow-net and can only be obtained by centrifuging samples of water, gave also some records of the occurrence of some of the larger forms which enables a comparison to be made between the plankton conditions in the English Channel and in the northern part of the Irish Sea.

---

* The salinity off Port Erin averages about 34·2 per mille. Its range for April, May, and June in the year when we took the most complete series of observations is from 34·02 to 34·4 per mille.

† Journ. Mar. Biol. Assoc. vol. xi. 2 (1917), p. 133.

There are certain differences in detail. For example, the total Diatom curve at Plymouth has three maxima or crests, in April, August, and October. At Port Erin the curve has only two crests, a much greater maximum in spring and a variable and smaller one in autumn, while Diatoms are usually wholly absent in August.

On the other hand, there is a general agreement in regard to the distribution throughout the year of many of the more abundant organisms. For example, amongst Diatoms *Coscinodiscus* is a winter and early spring form, *Biddulphia* flourishes throughout the winter from November to April or May, *Rhizosolenia* is a summer form having its maximum in June, while *Chætoceras* and *Lauderia* have two maxima, the one in spring and the other in autumn, in the English Channel and the Irish Sea alike. Amongst Copepoda there seems to be a general agreement along with a certain amount of difference in detail which will be referred to below when discussing the species.

I may recall that in November 1910 I read a paper before this Society * in which I made a comparison between the summer (July) plankton on the West Coast of Scotland and that of the Irish Sea, showing that in some of the deep fjord-like highland sea-lochs green-coloured phytoplankton can be obtained even in the height of summer, while a zooplankton may be found living in abundance a few miles away. This, of course, would be impossible in the Irish Sea, where a zooplankton and a phytoplankton do not occur simultaneously.

DIATOMS.

The seven generic forms I have selected for consideration taken together make up nearly the whole of the Diatom plankton of the year. No other genus occurs in anything like such profusion as these. In April, for example, when the Diatoms are usually at their climax, all the remaining genera (at most 10 or 12) taken together make up only about one-thousandth, or less, of the whole. Moreover, these common Diatoms often attain their greatest profusion successively, not simultaneously, so that single genera, or it may be single species of a genus, make up on occasions the bulk of the phytoplankton. For example, in May 1916 the month's average haul of Diatoms was 7,171,789, while the average for the genus *Chætoceras* taken alone was 6,947,333, leaving only 224,456 as the average of all the rest of the Diatoms. On the last two individual hauls, taken on May 25th and 29th, the actual numbers were as follows:—

Chætoceras alone	24,094,500 ...	19,461,600
C. sociale alone	23,936,000 ...	19,396,000
All other Diatoms together...	166,300 ...	228,900

So that on these occasions, and they are examples of many, one species makes up nearly the whole of the plankton.

---

* Journ. Linn. Soc., Zool. xxxii. (1913) p. 23.

The maximum on the Diatom curve ranges from March to May. In 1907 it was in March, in 1908 in May, and in 1909 in April. In some years the Diatom maximum may be divided into two parts, an earlier due mainly to *Chætoceras* and *Thalassiosira*, and a later in June due to *Rhizosolenia* and *Guinardia*. A common order of succession for the species which contribute most largely to the Diatom maxima is—*Biddulphia mobiliensis* and *Coscinodiscus radiatus* in early April, *Chætoceras debile* in late April, *Chætoceras sociale* in May, *Chætoceras teres* and *Rhizosolenia Shrubsolei* in early June, and *Rhizosolenia* (several species) and *Guinardia* in later June. The autumn Diatom maximum is constituted mainly in the Irish Sea by *Chætoceras subtile* and *Rhizosolenia semispina*. Certain species of most of the genera we are dealing with are commonly regarded as "oceanic" in the sense that they are characteristic of the open sea, although they may occasionally be carried in shore and so form a part of the coastal plankton; while other species are "neritic," having their origin and their home in coastal waters and not being found normally in the open ocean. For example, *Chætoceras densum*, *C. boreale*, *Coscinodiscus radiatus*, and *Rhizosolenia semispina* are supposed to be oceanic; while *Biddulphia mobiliensis*, *Chætoceras subtile* (and other species), *Coscinodiscus concinnus*, *Rhizosolenia setigera*, and *Lauderia borealis* are probably neritic. Other species of these genera are of doubtful position in this classification, or it may be are "panthalassic" or equally at home in both regions.

BIDDULPHIA.

This is a winter and early spring group of Diatoms, generally appearing in September or October, becoming more abundant in November and reaching a maximum in March or April. It dies off during May, and is practically absent in June, July, and August.

The species, or forms, that occur in our plankton are *Biddulphia mobiliensis* (?*B. regia*) and *B. sinensis* (fig. 3). This is one of the cases where there is some difference of opinion as to the validity of species. Whether *B. regia* is only a form of *B. mobiliensis*, and what is the exact relation of *B. sinensis* to the others, has been and may still be a matter of discussion. Specimens can be picked out that seem distinct and characteristic, but others occur in nature that are intermediate and possibly abnormal *.

B. sinensis is an exotic, oceanic form which, according to Ostenfeld, made its appearance at the mouth of the Elbe in 1893, and spread during successive years in several directions. It appeared suddenly in our plankton gatherings at Port Erin in November 1909, and has been present in abundance each year since. Ostenfeld, in 1908, when tracing its spread in the North Sea, predicted that it would soon be found in the English Channel. Miss Lebour, who has recently examined the old plankton gatherings at the Plymouth

---

* See forms figured in Trans. Biol. Soc. Liverpool, xxvii. (1913) p. 210.

Laboratory, finds that as a matter of fact this form did appear in abundance in the collections of October 1909, within a month of the time when according to our records it reached Port Erin. Whether or not this species was brought accidentally by a ship from the far East, there is no doubt that it was not present in our Irish Sea plankton gatherings previous to 1909, but has been abundant since that year, and has completely adopted the habits of its English relations—appearing with *B. mobiliensis* in late autumn, persisting during the winter, reaching a maximum in spring, and dying out before summer. *Biddulphia* is generally the first Diatom to show a marked increase in early spring, and is responsible for the moderate rise in the curve which takes place in February or March.

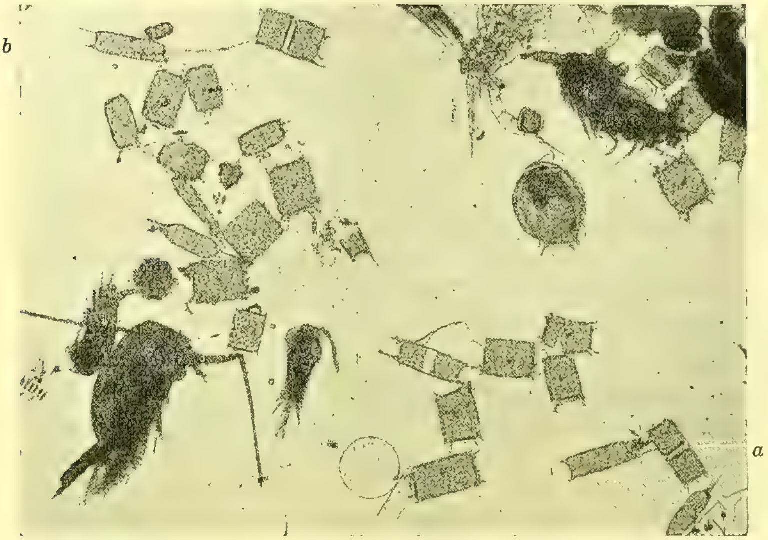

Fig. 3.—Photo-micrograph of a plankton preparation showing (*a*) *Biddulphia mobiliensis*, forma "*regia*," and (*b*) *B. sinensis.*

Our largest records of *Biddulphia* are as follows :—

From three hundred thousand to over six hundred thousand per haul on several occasions between middle of March and middle of April in 1910 and 1911, and towards end of April and beginning of May, 1916.

From three hundred thousand to over seven hundred and fifty thousand on ten occasions between November 10th and 27th, 1911, 1914, and 1915.

The highest monthly averages in the early spring months occur as follows :—

February ...	in 1907 and 1912.
March ..	in 1910, 1911, 1914, and 1915.
April ...	in 1908, 1909, 1913, and 1916.

A second, usually slighter, maximum occurs in November, when the numbers are higher than in December and January ; but on three occasions

(1911, 1914, and 1915) in our ten years the November monthly average is the highest in its year. Moreover, two of these November records, viz., 341,231 in 1911 and 406,100 in 1914, are the highest in the whole series. So *Biddulphia* may be regarded as characteristic of the late autumn (November) as well as the early spring plankton.

COSCINODISCUS.

The more abundant species that our records deal with are *Coscinodiscus concinnus*, *C. Grani*, and *C. radiatus*. They are mainly winter and spring forms, the maximum of the genus occurring always in our experience in either March or April. *Coscinodiscus* (fig. 4) agrees very closely with *Biddulphia* in its distribution throughout the year, beginning in late autumn, maintaining its position throughout the winter, increasing in January or February, and then more rapidly in March and April, and dying away before the height of the summer; but it sometimes continues to be present in small quantities further into the summer months than is the case with *Biddulphia*.

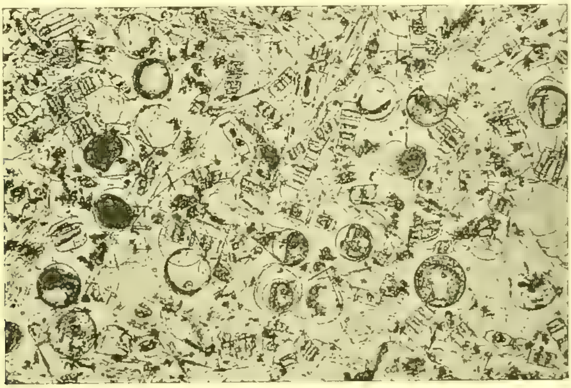

FIG. 4.—Photo-micrograph of an early spring phytoplankton consisting mainly of *Coscinodiscus* and *Biddulphia*.

The presence of *Coscinodiscus* in quantity in the spring plankton is easily seen through a glass jar with the unaided eye, as the little rounded drum-like cells give a characteristic granular appearance to the gathering.

Our largest records of *Coscinodiscus* are :—

From four to five hundred thousand per haul on several occasions between middle of March and middle of April, 1911, 1912, 1913, 1915, and 1916.

About nine hundred thousand on several occasions at end of April 1914.

From one million to close on five millions on two occasions in middle of April 1915.

So *Coscinodiscus* may outrival its companion form *Biddulphia* at the time of the vernal maximum, but does not attain to such high numbers in late autumn. The October and November monthly averages never, in our series of years, come anywhere near the averages for March and April.

Both *Biddulphia* and *Coscinodiscus* seem to be slightly later in their maxima in the Irish Sea than in the English Channel, judging from the Plymouth records.

In the years 1907 to 1912, inclusive, the highest monthly averages (March and April) for *Coscinodiscus* run in general about 100,000. In 1913 and 1916 they are close on 200,000, in 1914 over 300,000, and in 1915 there is a sudden jump, in April, to over 840,000. The other months of that year do not show unusually high numbers.

CHÆTOCERAS.

The chief species of this genus in our Irish Sea plankton are *Chætoceras boreale*, *C. contortum*, *C. criophilum*, *C. debile*, *C. decipiens* (fig. 6), *C. densum*, *C. diadema*, *C. sociale*, and *C. teres*. Of these, *C. boreale*, *C. criophilum*, and *C. decipiens* are Arctic oceanic forms, *C. densum* is a temperate oceanic or

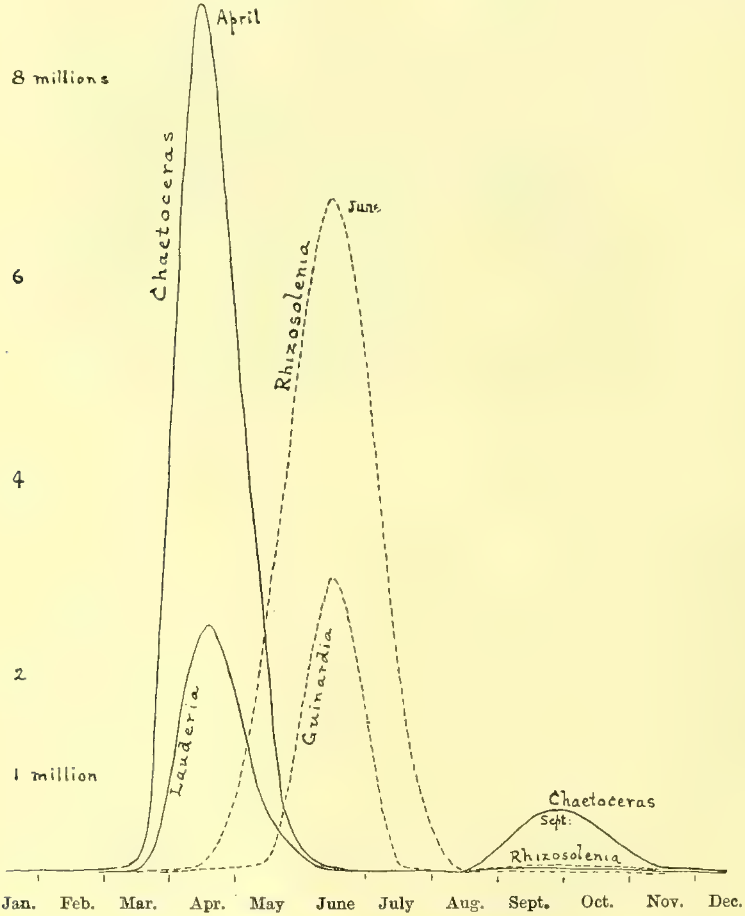

FIG. 5.—Curves of the more important Diatoms of the April and June maxima.

Atlantic species, and all the rest may be classified as temperate neritic. Some of these (*C. criophilum*, *C. debile*, *C. decipiens*, *C. sociale*, and *C. teres*) are spring forms with a maximum in April or May, while *C. boreale* and *C. densum* are autumn species having their maxima in September or October. Consequently the genus is well represented throughout a considerable part of the year, and the numbers are very high in April and May, and sometimes also in September and October (see curve, fig. 5). A few of our highest records for the genus, giving the nearest million in each case, are :—151 millions on May 4th, 1914, 95 millions on April 29th, 1912, 68 millions on May 16th, 1911, 49 millions on April 22nd, 1910, and 44 millions on May 19th, 1911. The highest record we have for the autumn species is 30 millions on September 26th, 1912. On May 16th, 1911, *C. debile* contributed 30 millions and *C. sociale* 12 millions to the total in the haul ; and on May 4th, 1914, *C. debile* gave 148 out of the 151 millions present. If we examine the records of the separate species for the year 1914 as an example, we find that *C. contortum* has an average of 62,700 per haul in May, *C. debile* an average of 867,878 in April and 18,972,800 in May (the record), *C. decipiens* an average of 821,311 in April and 321,050 in May, *C. sociale* an average of 1,229,500 in May, *C. teres* an average of 577,867 in April ; while of the autumn species *C. boreale* has an average of 53,200 in September and 54,644 in October, and *C. densum* has 151,120 in September and 100,624 in October. *C. debile* and *C. decipiens* were also very abundant that October.

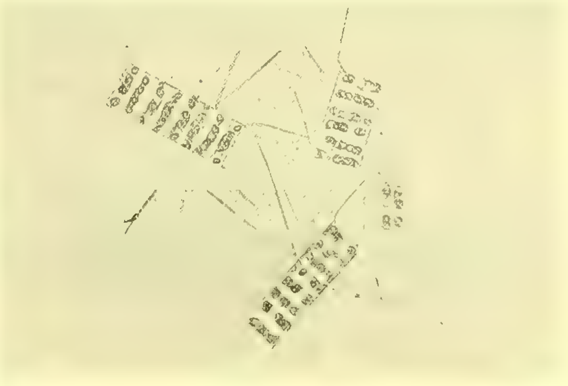

FIG. 6.—*Chætoceras decipiens*, showing the active winter growth. From a photo-micrograph by A. Scott.

The highest monthly averages for *Chætoceras* fall as follows during our ten years :—

March ... in 1907.
April ... in 1909, 1910, and 1912.
May ... in 1908, 1911, 1913, 1914, 1915, and 1916.

The highest average is nearly 23 millions, in May 1911. None of the September and October averages run as high as those in spring, and only two reach millions, viz., 3,956,047 in October 1911, and 7,702,658 in September 1912. The years 1911 and 1912 had high numbers of *Chætoceras* throughout many of the months *. There are no months in the ten years when *Chætoceras* was totally unrepresented; but July and August show the lowest averages—the lowest of all being only six individual cells in August 1907.

LAUDERIA.

We have only the one species, *Lauderia borealis*, Gran (fig. 7), in our records. It is a late spring or early summer form, occurring generally from March or April to June or July, with a later, smaller, occurrence in autumn. It is sometimes present in large quantities, *e. g.*, 20,064,000 on April 22nd, 1910; 12½ millions on April 29th, 1912; 3,600,000 on May 4th, 1914. The maximum is towards the end of April or beginning of May, when *Lauderia* helps, along with *Chætoceras*, to form the main crest on the vernal Diatom curve (see fig. 5).

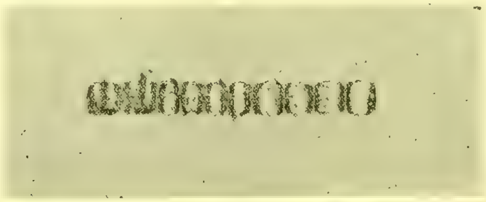

FIG. 7.—Photo-micrograph showing a chain of *Lauderia borealis.*

THALASSIOSIRA.

The only species of this genus that are of any importance in our records are *T. gravida*, Cleve, and *T. Nordenskioldi*, Cleve (fig. 8). Apparently *T. gravida* is the only one common at Plymouth, but *T. Nordenskioldi*, along with *Chætoceras contortum* and *C. debile*, helped to constitute the vernal maximum at Port Erin in 1907, and has been still more abundant on several occasions since. *T. Nordenskioldi* is in the main a neritic, arctic or Scandinavian species, and probably its occasional occurrences in quantity are to be regarded as invasions of some arctic water and northern plankton into our British seas. In April 1917, it was abundant at Port Erin along with *Chætoceras teres*, *C. debile*, and *C. decipiens*.

All our high records (over a million per haul) for *Thalassiosira* lie between late in April and late in May, and the two highest are six millions on April 29th, 1912, and six and a half millions on May 16th, 1913. Other high records have occurred during these same months, in 1910, 1911, 1912, 1913, 1914, 1915, and 1916.

---

* The largest hauls of Diatoms as a whole, all species taken together, were in May of 1912 and 1913 (see Table on p. 188).

The highest monthly averages for *Thalassiosira* are 721,000 in April 1912, 898,000 in May 1913, and 976,000 in May 1915. The genus is totally absent from our records throughout the ten years in December, January, and February, and again in July and August, and is very poorly represented in several other months. In fact, it is only really abundant in April and May and not always then. In this distribution over the months of the decade this genus forms a marked contrast with *Chætoceras*, which is so constantly present.

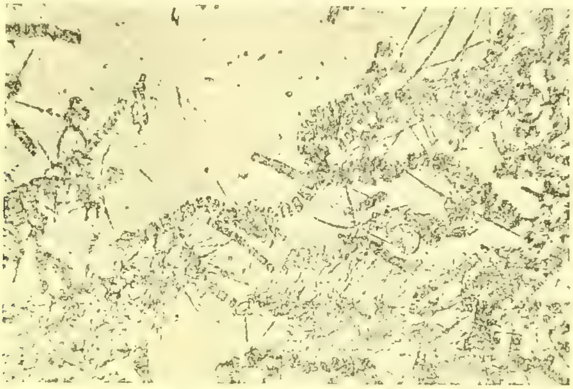

FIG. 8.—Photo-micrograph of a phytoplankton consisting mainly of *Thalassiosira Nordenskioldi.*

RHIZOSOLENIA.

The species that occur most abundantly in our records are *Rhizosolenia semispina*, *R. Shrubsolei*, *R. Stolterfothi* and, less abundantly, *R. setigera* and *R. alata* (rarely). The two last named are temperate Atlantic forms, and *R. semispina* is a typically arctic oceanic species.

They are all summer or autumn species, the genus being often quite unrepresented in certain of the winter months. It usually begins to appear in the nets in February and reaches its maximum in June. The numbers are sometimes enormous, giving the water in a glass jar a characteristic silky or fibrous appearance and causing the June crest that is usually present as a distinct elevation on the Diatom curve (see fig. 5, p. 182).

The most abundant species in the Irish Sea is *Rhizosolenia Shrubsolei*—at Plymouth it is *R. Stolterfothi* ; but *R. semispina* (fig. 9) is sometimes present in abundance at Port Erin in autumn, causing a second crest or maximum in September or October. In September 1907, thirteen millions and sixteen millions of this species were taken in two hauls of the surface-net at Station III. (three miles off Port Erin), while the following year, at the same time and locality, it was almost absent.

We have had much larger numbers, of *R. Shrubsolei*, in June; and amongst our largest records of the genus taken as a whole are:—184 millions on May 30th, 173 millions on June 3rd, 59 millions on June 8th, 43 millions on June 13th, all in 1912, and 17 millions on June 21st, 1915.

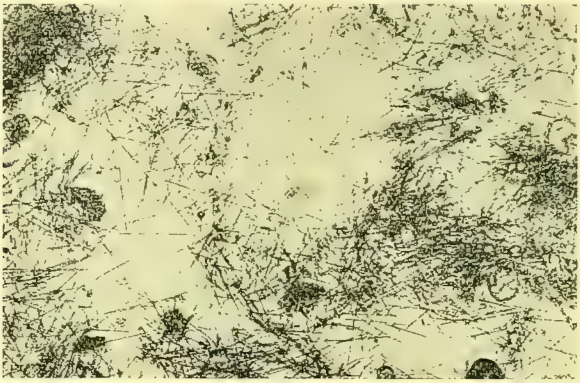

FIG. 9.—Photo-micrograph of a phytoplankton consisting mainly of *Rhizosolenia semispina*.

The highest monthly average is in June in all of our years except 1907 when it was in May, and 1913 and 1916 when it was in July. The greatest average recorded is over 40 millions in June 1912.

The autumn records are very irregular and sometimes show no rise whatever. Even when present it is slight compared with the June maximum (see fig. 5, p. 182). The highest monthly average in autumn is 117,122, in September 1912.

GUINARDIA.

Only the one species, *Guinardia flaccida*, occurs in our records (fig. 10). It is a summer form occurring mainly between April and July, with the maximum almost invariably in June. Our largest records are 22,800,000 on June 3rd, 1912; 18,000,000 on May 30th, 1912; and 8,773,000 on June 11th, 1910. We have several records of over 7,000,000 early in June, one of over two millions on July 8th, 1913, and one of over a million as late as July 16th, 1916.

Guinardia, when present, makes up along with *Rhizosolenia* the June elevation, which is sometimes so marked towards the end of the vernal Diatom maximum. This last summer (1917) it was unusually late, showing a maximum of five millions on 23rd July, along with one million of *Rhizosolenia*.

The highest monthly averages are all in June with the exception of 1916, when it was in July. The greatest recorded average is close on six millions for June 1912. The lesser, secondary, increase in autumn has its highest point in September—the greatest recorded monthly average being 10,967 for September 1912. It is interesting to notice that according to Pavillard *Guinardia flaccida* is abundant in the Gulf of Lyons as late as October.

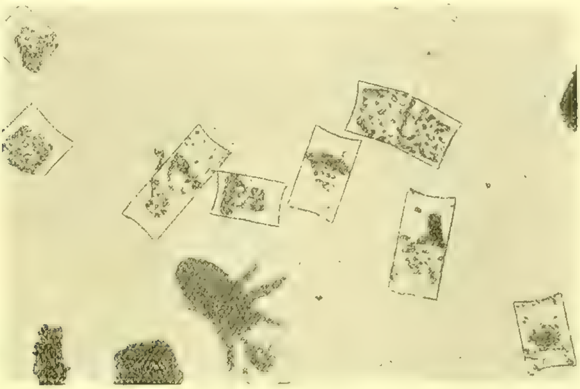

FIG. 10.—*Guinardia flaccida*, from a photo-micrograph by A. Scott.

TABLE

showing the monthly averages of the selected Diatoms throughout a year.

1912.	*Biddulphia.*	*Chætoceras.*	*Coscinodiscus.*	*Rhizosolenia.*	*Thalassiosira.*	*Guinardia.*	*Lauderia.*
Jan.....	24,920	7,342	9,877	22	0	257	189
Feb. ..	36,885	10,301	10,034	12	0	105	0
Mar. ..	21,176	3,977,292	95,446	525	25	162	337
Apr. ..	21,869	18,365,750	100,619	36,464	721,338	3,158	1,622,478
May ..	1,072	2,844,861	14,586	22,008,744	41,033	2,789,433	170,878
June ..	0	67,543	0	40,833,771	0	5,919,429	0
July ..	0	39,527	56	1,228	0	158	0
Aug. ..	11	694,961	0	13	0	0	0
Sept. ..	4,131	7,702,658	1,677	117,122	3,978	10,967	8,944
Oct.....	5,827	214,421	11,914	820	57	2,176	29
Nov. ..	25,714	9,476	5,436	0	0	21	0
Dec. ..	8,059	1,106	1,573	0	0	141	0

The above table shows very clearly how these important genera reach their maxima at different times, and how, for example, *Chætoceras* in spring (April) gives place to *Rhizosolenia* and *Guinardia* in early summer (May and June). Curves can be drawn mentally from a glance at the columns of figures which will demonstrate the waxing and waning of the several types.

The following table showing the largest hauls of total Diatoms and of total Copepoda in each of the ten years brings out well how greatly the Diatoms outnumber the Copepoda—in some cases in the proportion of about a thousand to one.

	Diatoms.		Copepoda.	
	Largest haul.	Date.	Largest haul.	Date.
1907	698,350	April 6th	28,900	Aug. 17th
1908	5,746,300	May 28th	68,015	Sept. 14th
1909	10,358,300	April 22nd	71,010	Oct. 18th
1910	70,128,400	April 22nd	119,650	Sept. 19th
1911	69,982,500	May 16th	248,045	July 18th
1912	202,993,600	May 30th	223,789*	May 20th
1913	205,814,700	May 16th	118,660	July 21st
1914	155,288,000	May 4th	217,571	Nov. 9th
1915	18,893,300	June 15th	117,340	Aug. 2nd
1916	24,260,800	May 25th	118,524	Sept. 25th
1917	64,339,250	May 3rd	147,706	July 19th

The relatively high records for Diatoms in 1912 and 1913 are due in the former case to the usual June maximum of *Rhizosolenia* and *Guinardia*, and in the latter case to a quite exceptional invasion of *Asterionella japonica*—the only occasion in our records when this genus has been abundant in the Irish Sea. We regard it as quite a rare form here. It is exceedingly abundant to the south of Iceland (Ove Paulsen) and also in the Gulf of Lyons (Pavillard).

COPEPODA.

The following table shows the total numbers recorded of our six important species of Copepoda in the years 1909 and 1910 :—

	1910.	1909.
Oithona helgolandica ...	872,678	465,066
Pseudocalanus elongatus	368,326	309,973
Acartia clausi ...	340,631	63,373
Paracalanus parvus ...	217,633	54,120
Temora longicornis ...	147,043	62,659
Calanus finmarchicus ...	15,418	21,412

---

* An exceptionally large haul at such an early date—due apparently to several moderately large swarms of different Copepoda occurring together, viz., *Calanus, Pseudocalanus, Temora,* and *Acartia.*

The actual detailed numbers are of no importance except as indications of the relative abundance of the species. It is clear that *Oithona* and *Pseudocalanus* (in 1909) far outnumber the others. *Acartia* shows a notable increase in 1910.

The Copepoda as a whole are a summer and autumn group, all the crests of their annual curves being found between May and October. Figure 11 shows curves of occurrence of the five most abundant of the above-named species for the year 1912, which may be regarded as typical. Curves of *Calanus* are shown separately in figure 12. The remaining one of our six selected species, *Calanus finmarchicus*, although much the largest individually and probably one of the most important from the fisheries point of view, only occasionally occurs in very large quantities in the Irish Sea, and its total numbers in a year are much below those of the other species, as the following table shows.

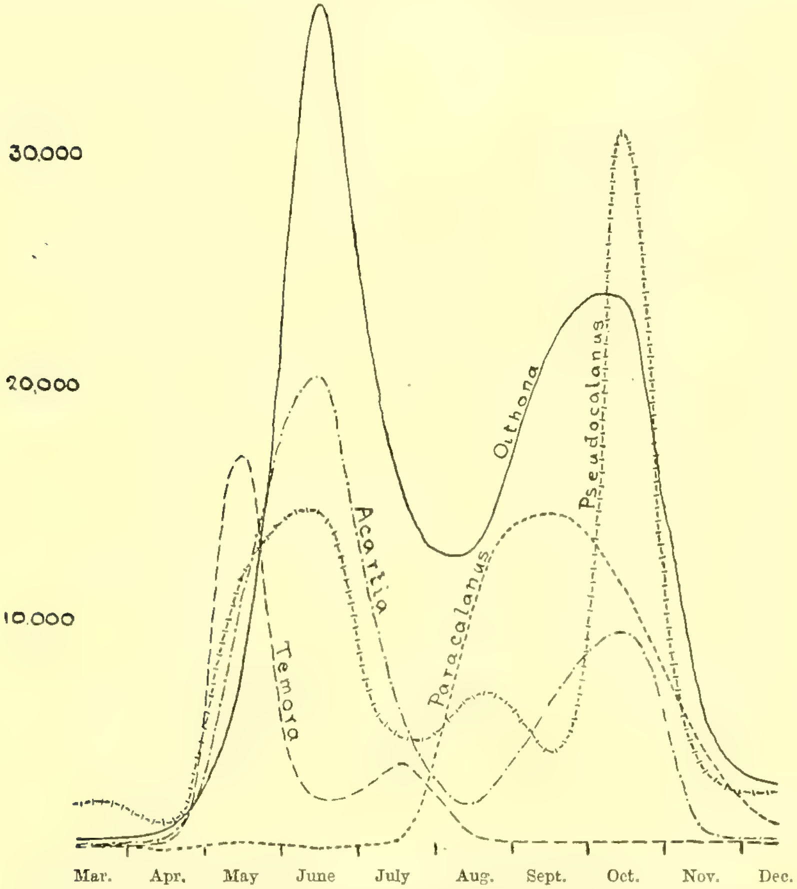

FIG. 11.—Curves of five most abundant Copepoda at Port Erin in 1912.

TABLE *showing the total numbers of the selected Copepoda recorded in the ten years.*

	1907.	1908.	1909.	1910.	1911.	1912.	1913.	1914.	1915.	1916.	Totals and averages over the 10 years.
No. of hauls ……	77	93	112	102	107	98	95	97	101	96	978
Oithona ……….	269,775	281,634	465,066	872,678	1,155,108	1,055,213	997,565	1,189,945	865,239	839,154	7,991,377
Average per haul ..	3,503	3,028	4,152	8,556	10,795	10,767	10,501	12,267	8,567	8,741	8,171
Pseudocalanus ….	113,337	177,592	309,973	386,326	365,983	643,466	500,650	487,383	788,174	679,259	4,452,143
Average per haul ..	1,472	1,909	2,768	3,788	3,420	6,566	5,270	5,025	7,864	7,076	4,583
Acartia ……….	52,211	113,923	63,373	340,631	323,633	450,778	401,305	236,985	309,110	222,729	2,514,678
Average per haul ..	678	1,225	566	3,340	3,025	4,600	4,224	2,443	3,060	2,320	2,571
Paracalanus ……	25,787	91,147	54,120	217,633	351,088	363,881	196,364	568,699	119,197	138,438	2,126,354
Average per haul ..	335	980	483	2,134	3,281	3,713	2,067	5,863	1,180	1,443	2,276
Temora ……….	104,093	20,495	62,659	147,043	106,359	210,542	144,624	146,707	118,218	146,174	1,206,914
Average per haul ..	1,350	220	559	1,442	994	2,148	1,522	1,512	1,170	1,523	1,234
Calanus ……….	21,352	19,646	21,412	15,481	5,843	79,429	23,183	42,494	13,119	18,031	259,990
Average per haul ..	277	211	191	152	55	810	244	438	130	188	266

CALANUS.

Calanus finmarchicus (Gunner)* is present throughout the year in the Irish Sea, and may be taken in small quantities at almost any time and in larger numbers on different occasions in different years. In 1907 it was fairly abundant (a few thousands in a haul) in April, and again at the end of July and the beginning of August, and in October. In 1908, on the other hand, the thousands per haul were not reached until later in the year, and the numbers remained relatively high from September to December (2,850 on December 23rd). In 1909, in addition to occasional thousands in May, June, July, and October, we have evidence of an unusually large swarm that entered the bay on July 17th and 19th, when hauls estimated at 20,000 each were obtained. The average for these three years shows maxima in July and October (see fig. 12).

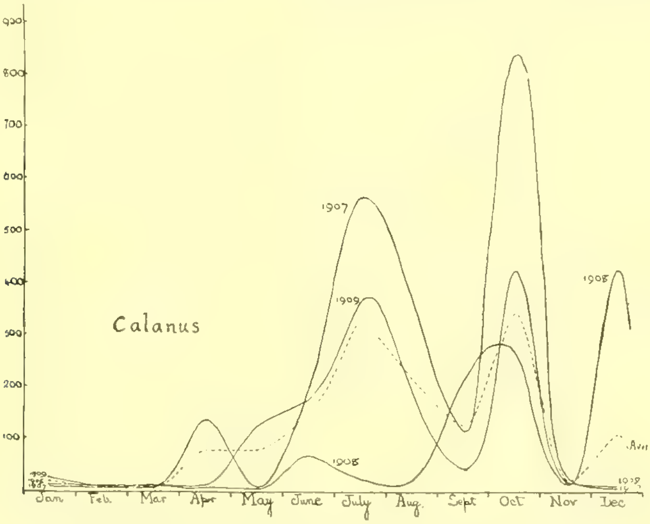

FIG. 12.—Curves of *Calanus* for three years (1907–9) at Port Erin, showing successive waves of invasion, 2 or 3 in each summer.

In 1910 there were no very large hauls, and the thousands were only reached at the end of July and the beginning of August—perhaps the most usual time for swarms to appear in the bay.

In 1911 the numbers in general were low, but two of the customary large swarms appeared in summer, one on July 4th and the other on July 18th.

In 1912 the numbers were higher again, and thousands occurred on various dates from April to October. The very high record of 50,720 was obtained on May 17th, unusually early for such a large swarm.

---

* I use this older specific name as I am inclined to agree with Wolfenden, Esterly and others that the characters used in the attempt to separate "finmarchicus" and "helgolandicus" as species are too slight and inconstant to be relied upon.

In 1913 the numbers were lower, and the maximum was 4000 on July 28th.

In 1914 the maximum was 7320 on August 6th.

In 1915 again the numbers were low, the highest being 3232 on July 1st.

In 1916 a swarm appeared in the bay on July 11th, when over 12,000 were taken in a haul. A few days before a similar haul gave only 10 specimens, and a few days after 200. The average per haul at Port Erin over the ten years is only 266.

On the whole this record agrees well with that at Plymouth, which is "Common on and off from the end of April to the beginning of November, generally present in small numbers at other times" (Miss Lebour).

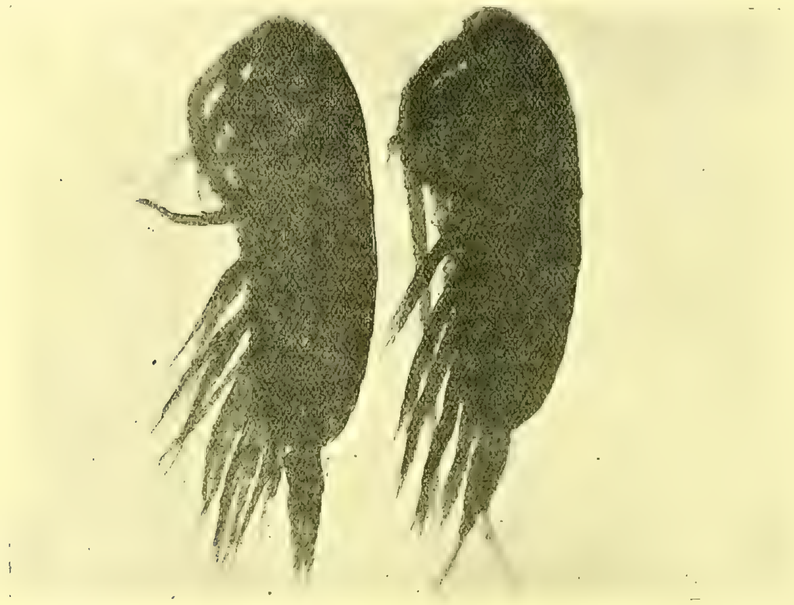

FIG. 13.—*Calanus finmarchicus*, from a photo-micrograph by A. Scott.

Calanus finmarchicus (fig. 13), as its specific name suggests, is a northern or Scandinavian form with a wide distribution through the colder waters of the North Atlantic. According to Ove Paulsen its home and centre of distribution lies to the south of Iceland.

In Loch Fyne on the west coast of Scotland, off Skate Island, *Calanus* appears to be present throughout the year in great quantities in deep water, at or near the bottom, along with *Euchæta norvegica* and *Nyctiphanes norvegica*. For example, in July 1907, off Skate Island in 104 fathoms, we caught 13,000 *Calanus* in one vertical haul, and on another occasion off East Loch Tarbert, in 76 fathoms, we got 10,000. We have also obtained from the yacht at various localities in the deep lochs on the west coast of Scotland large hauls of *Calanus* by means of vertical hauls when no specimens were obtained at the surface. In fact this Copepod seems to be permanently present in the deeper waters of these lochs.

In addition to these deep water specimens of *Calanus* we find on occasions, on the west coast of Scotland, large swarms on the surface, which may be the result of invasions from the ocean, and there is a considerable amount of evidence that such swarms are the cause of local mackerel fisheries.

Some years ago (1909) Dr. E. J. Allen and Mr. G. E. Bullen published* some interesting work, from the Plymouth Marine Laboratory, demonstrating the connection between mackerel and *Calanus* and sunshine in the English Channel; and Farran† states that in the spring fishery on the West of Ireland the food of the mackerel is mainly composed of *Calanus*. In the summer of 1913 we had an experience at Tobermory, in Mull, which I shall quote from two letters written from the yacht at the time, and published in 'Nature.'

"S.Y. 'Runa,' Tobermory, July 12th, 1913.

"On arriving in this bay last night we found that the local boats had been catching abundance of mackerel close to. We bought some for supper (good fish for a halfpenny each), and on dissection found that the stomachs of all of them were crammed full of fresh-looking *Calanus* (the individual Copepods being for the most part distinct and perfect), along with a few immature *Nyctiphanes* and larval Decapods. Professor Newstead and my daughter then noticed, while fishing over the side of the yacht, about 8 p.m., that the gulls in the bay were feeding in groups around patches of agitated water evidently caused by shoals of fish. On rowing out to these we saw distinctly the mackerel, large and small, darting about in great numbers in the clear water, and we also noticed every here and there on the smooth surface of the water—it was a beautifully calm evening—innumerable small whirls or circular marks which, looking closely, I found to be caused by large Copepoda close to the surface.

"About twenty years ago I sent a note to 'Nature,' from the yacht 'Argo,' in regard to large Copepoda (I think it was *Anomalocera* on that occasion, and the locality was further north, off Skye), splashing on the surface so as to give the appearance of fine rain; and this present occurrence at once reminded me of the former occasion, but here the Copepod was *Calanus finmarchicus* of large size and in extraordinary abundance. They could be clearly seen with the eye on leaning over the side of the boat, a small glass collecting jar dipped at random into the water brought out twenty to thirty specimens at each dip, and a coarse grit-gauze tow-net of about 30 cm. in diameter caught about 20 cubic centimetres of the Copepoda in five minutes.

---

* Journ. Mar. Biol. Assoc. vol. viii. (1909) pp. 394-406.

† Conseil Internat. Bull. Trimestr. 1902-8, Planktonique, p. 89.

The mackerel were obviously darting about, occasionally leaping to the surface (which gave the gulls their opportunity) where the whirls, caused by the Copepoda, were thickest, and an examination of the stomach-contents of the fish on the yacht afterwards, showed us that the amount in one mackerel was about the same quantity as that caught by the tow-net in five minutes. Professor Newstead and I have made a count of 8 c.c. of the tow-net gathering, and estimate that it contains about 2400 specimens of *Calanus*. This would give about 6000 Copepods in the stomach of an average mackerel, or in a five-minutes' haul of the tow-net, on this occasion.

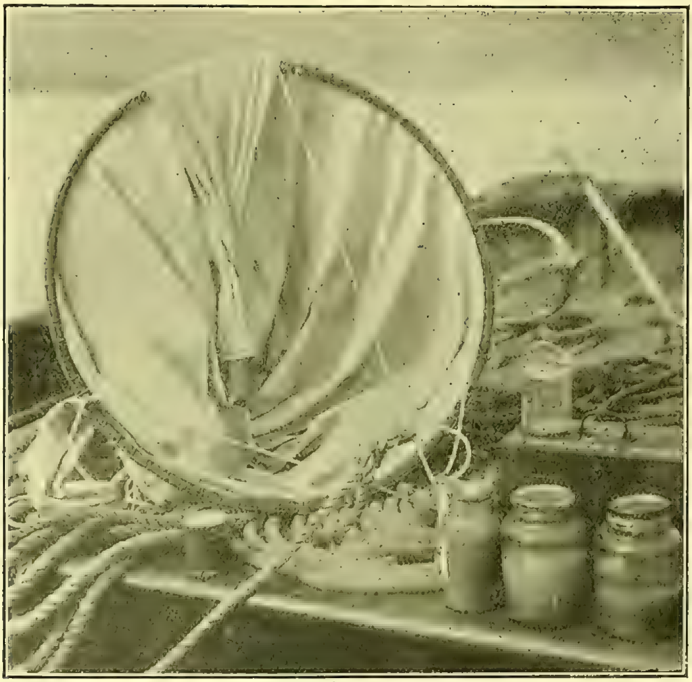

FIG. 14.—Photograph of exceptionally large hauls (about 1000 c.c. in a jar) of *Calanus* taken from the yacht 'Runa' in 1913 on the west coast of Scotland. The largest haul was estimated to contain at least half a million individuals.

"It may be added that these mackerel were evidently not being nourished in accordance with the views of Pütter, and were clearly able to fill their stomachs from the plankton around them.". . . .

The following note, written some weeks later, records the conclusion of the matter, so far as that summer's observations went :—

"S.Y. 'Runa,' off Island of Eigg, August 12th, 1913.

"On getting back to Tobermory on Saturday, we found the plankton to be in marked contrast to its condition four weeks ago. The vast swarm of

Calanids has gone, and there are now no signs of mackerel feeding in the bay. In fact, the change has been noticeable for some days in the seas outside, and we have not been getting lately the large plankton catches that were usual in the latter half of July. On July 14th a haul of the large surface tow-net, in the open sea off Ardnamurchan, gave such a huge catch of *Calanus* (about 1000 c.c.) that we promptly took a second similar haul, and had it cooked as a sort of potted 'shrimp' confection for tea (sampled by ten persons, including the crew, who were much interested to try this new edible 'fish'); while on August 11th a haul of the same net, taken at the same spot, gave only a small catch of some 15 c.c., containing very few Calanids, along with the usual scanty summer zooplankton." . . . .

The importance of *Calanus* as a food for migratory pelagic fishes such as the mackerel cannot be doubted (see fig. 14).

PSEUDOCALANUS.

Pseudocalanus elongatus (Boeck) is widely distributed in the North Atlantic and is present in the Irish Sea throughout the year (fig. 15). It reaches its lowest level in January and February, and has its maximum in late summer and autumn (June to October in our records, generally September or October).

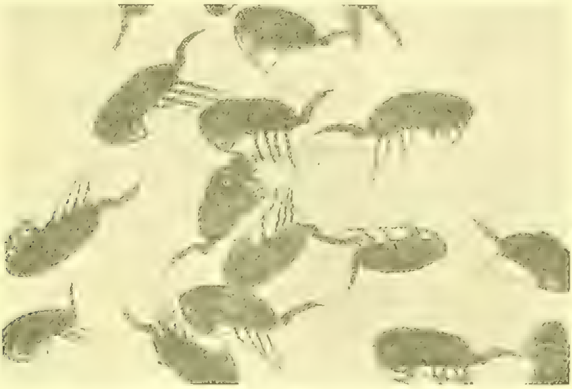

FIG. 15.—*Pseudocalanus elongatus*, from a photo-micrograph by A. Scott.

This Copepod comes next after *Oithona* as the second most abundant species in the Irish Sea, its average per haul over the ten years being 4583.

Some of the most important records are:—65,200 on May 20th, 1912; 91,960 on October 21st, 1912; 68,120 on June 24th, 1913; 60,600 on May 5th, 1916; 59,600 on September 25th, 1916; 58,200 on October 31st, 1912; 54,350 on July 31st, 1911; and many other records between 35,000 and 50,000 in these same months.

PARACALANUS.

Paracalanus parvus (Claus) is a southern form (fig. 16) which extends to the tropics and has a wide distribution. It is present in quantity only during autumn and winter in the Irish Sea, being practically absent between February and July, and having its maximum in September or October. The largest hauls are in autumn, for example, 59,460 on September 7th ; 138,300 on September 10th ; 53,500 on September 15th, all in 1914 ; 61,930 on August 24th, 1911 ; 49,800 on September 8th, 1910 ; 49,390 on September 7th, 1912 ; 44,060 on October 24th, 1912 ; while other large hauls in the same months range from 25,000 to 40,000.

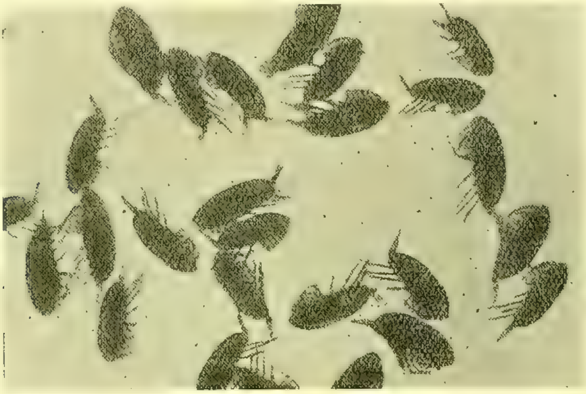

FIG. 16.—*Paracalanus parvus*, from a photo-micrograph by A. Scott.

This is a species that has varied considerably in quantity from year to year, its average per haul ranging from 335 in 1907 to 5863 in 1914. In the present year, 1917, it was especially abundant at Port Erin in September, along with *Oithona*.

OITHONA.

Oithona helgolandica (= *O. similis*), Claus, is the most generally abundant Copepod throughout the year in the Irish Sea ; but the months when it is taken in greatest numbers are June to November (inclusive) with the maximum generally in July. There may, however, be a second maximum later, in October or November.

The following may be quoted as exceptionally large hauls :—The highest, 225,450, is on July 18th, 1911, and the next highest, 199,300, is on November 9th, 1914 ; then we have 93,580 on July 28th, 1913, 87,530 on September 26th, 1912, and 83,550 on June 14th, 1910. We have twenty other records of over 44,000 each scattered over the months June to November. This is the Copepod which has the highest average number per haul over the ten years, viz., 8171 (see table, p. 190). Although this is a small species (fig. 17), still from its very great abundance it must be of considerable economic importance as a food-matter in the sea.

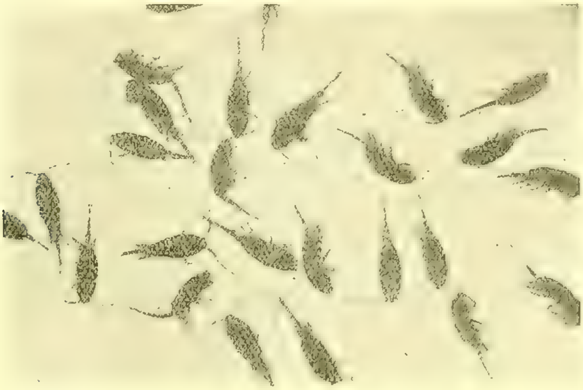

FIG. 17.—*Oithona helgolandica,* from a photo-micrograph by A. Scott.

ACARTIA.

Acartia clausi, Giesbr., is a summer species widely distributed over the North Atlantic, and present in greatest abundance in the Irish Sea from May to October (inclusive), and having a maximum generally in June, with another slighter rise in autumn, September or October.

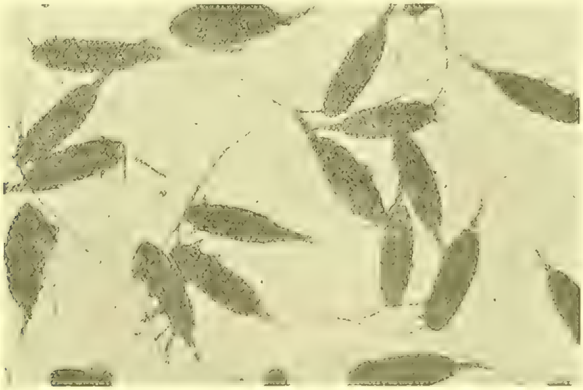

FIG. 18.—*Acartia clausi,* from a photo-micrograph by A. Scott.

The following are some of our highest records:—59,490 on June 27th, 1912; 59,360 on August 24th, 1911; 52,200 on May 20th, 1912; 50,100 on June 2nd, 1913; 44,000 on September 29th, 1913; and 41,950 on June 17th, 1912. The average of this species per haul throughout the ten years is 2571. Swarms of this oceanic species (fig. 18) in summer may possibly be connected with an inflow of Atlantic water; but probably also large numbers appearing locally in enclosed areas may be the result of reproduction and development *in situ*.

In some cases *Acartia* has been found in unusual abundance quite close to the shore, and even in water of low salinity.

Towards the end of September, 1917, we emptied for cleaning purposes the large open-air fish-ponds at the Port Erin Biological Station, and when most of the water had been pumped out we noticed that what remained was swarming with small Copepoda. Every bucket and jarful that one removed for inspection was found to be densely crowded—as densely, in fact, as an average jar of plankton representing the contents of a standard haul. Some buckets of these Copepoda were used for feeding the lobster larvæ and some of the smaller fish and other animals in the Aquarium, and a small sample that was preserved was found to be a practically pure gathering of *Acartia clausi*. One specimen of *Centropages* was present in the tube amongst many thousands of *Acartia*, when Mr. Scott took the photo-micrograph shown in fig. 18.

TEMORA.

Temora longicornis (Müll.) is a very local species, which may be found on occasions swarming in great abundance in small areas of the sea, generally close to land. It is a summer species and its maximum is generally in June or July, but was in May in 1912, when the large hauls of 50,400 and 83,400 were taken on the 17th and 20th respectively. Other large hauls of this

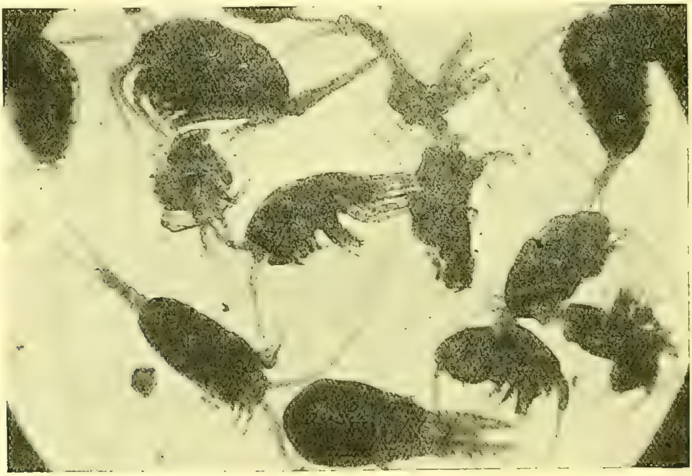

FIG. 19.—*Temora longicornis* from the stomach of a Mackerel. From a photo-micrograph by A. Scott.

species in our records are :—45,530 on July 11th, 1916 ; 43,800 on June 11th, 1913 ; and 34,665 on July 26th, 1910. The average for this species per haul throughout the ten years is 1234.

Temora (fig. 19) is characteristic of coastal as opposed to Atlantic water, and is the only "neritic" form in our series. The other five are all usually classed as "oceanic," but as I have pointed out above most of them are really present throughout the year in the Irish Sea.

Temora longicornis is on occasions one of the most abundant of our Copepoda in the Irish Sea and must be of considerable importance as a food for fish and especially for the herring in summer. In the latter part of July and the first half of August, 1917, the shoals of herring to the west of the Isle of Man came unusually close to land and even penetrated into bays and creeks ; and during this time they were feeding mainly, if not wholly, on *Temora*. Late in July this Copepod was so abundant that its presence caused large patches of a red colour on the surface of the sea off Port Erin and around the Calf Island. These red patches were noticed by the fishermen, and were spoken of amongst them as being "fish-food" or "spawn." A large jarful from such a red patch, obtained by one of the fishermen, was brought to the laboratory and found to be swarming with small Copepoda, which on examination proved to be almost wholly *Temora longicornis* (fig. 20). About one-fourth part of the contents of the jar was preserved, and on being counted later on was found by Mr. Andrew Scott to amount to 50 c.c. of Copepoda, consisting of 33,340 *Temora* and 2 *Calanus*. Mr. Scott estimated the oil present in 9 c.c. of the dried *Temora* at 2·47 per cent. of the weight, which was 0·925 gramme.

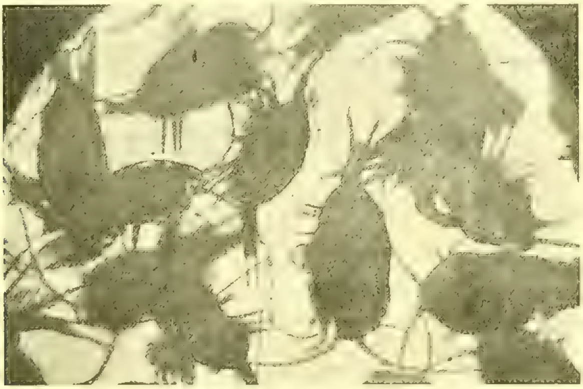

FIG. 20.—*Temora longicornis* from the "red patches." From a photo-micrograph by A. Scott.

During this same time the men were catching herring in quantity unusually close inshore in the neighbourhood of the red patches, and on examining, in the laboratory at the Biological Station, the stomach-contents of a number of these herrings, I found in every case that the stomach contained a mass of red material which was obviously, under the microscope, the broken-down remains of Copepoda. A few Crab zoea were recognisable, but the bulk of the material consisted undoubtedly of the Copepoda. Mr. Scott examined 5 c.c. of the stomach-contents for me, and found that it contained 975 easily recognisable specimens of *Temora*. A photograph (fig. 21), which Mr. Scott has made from one of the microscopic preparations, shows appendages that undoubtedly belong to this Copepod, while here and there in the stomachs complete specimens of *Temora* are to be seen. It is not possible to doubt that during these weeks, at the height of the summer herring fishery in the Irish Sea, the fish were feeding mainly upon this species of Copepod.

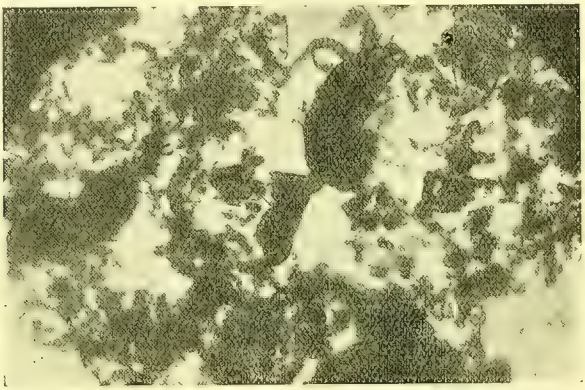

FIG. 21.—*Temora* remains from the stomachs of the Herring. From a photo-micrograph by A. Scott.

We recorded a similar occurrence off the Lancashire coast a few years ago, when in July 1913, at the time of an abundant mackerel fishery off Walney Island, the stomachs of some of the fish were found to be full either of *Temora* alone or of *Temora* mixed with *Isias* and a few other Copepoda (see fig. 19, p. 198). A few herrings from the Port Erin fishery of July 1916 were found by Mr. Scott to be feeding mainly on *Calanus*.

CONCLUDING REMARKS.

Many food-fishes are known to feed upon Copepod plankton during at least some portion of their life. The Loch Fyne herrings are frequently at the time of a fishery found to have their stomachs filled with *Euchæta* or *Calanus*. Mackerel, in the English Channel and to the S.W. of Ireland and elsewhere, have been recorded as feeding on *Calanus*. It has been shown in this paper that in Hebridean Seas the mackerel and in the Irish Sea herrings, at a time when they are present in great abundance, are feeding on some prevalent form of Copepod, such as *Calanus* or *Temora.* Other similar cases could no doubt be quoted and are known to marine biologists.

Then, as to demersal fish—young plaice, after their metamorphosis, feed chiefly on the smaller Copepoda, while in younger stages the post-larval plaice feeds upon Diatoms. We have noticed at the Port Erin Biological Station the post-larval plaice with its stomach showing of a golden brown colour from the Diatoms with which it was filled, and we have watched in a shallow pond the metamorphosed young plaice darting backwards and forwards pursuing, catching, and devouring the individual Copepoda. It is known that these Copepoda in their turn feed in part at any rate on Diatoms, so our two main constituents of the plankton are undoubtedly concerned in the nourishment of either young or adult fishes useful to man.

The association of shoals of fish with abundance of plankton is the result of the fact that, in order to get an adequate quantity of planktonic food, the fish must seek out and capture the Copepoda. In other words, the fish must go where the plankton is abundant and must in its movements follow the movements of the shoals of Copepoda. It is the very poverty of the plankton in some sea-areas, insisted on by Pütter, Lohmann and others, which makes it necessary for plankton-eating fish to move about in search of more abundant supplies.

Consequently it is of importance to show, as we now can, that in our coastal seas at least, where the fisheries we are interested in take place, the plankton is not uniformly distributed. Many of the Copepoda occur very definitely in local swarms, and various localities and depths are characterised at the different seasons by particular assemblages of plankton. It is therefore reasonable to believe, in view of the facts given above as to the association of fish and plankton, that these variations in the distribution must have a marked effect upon the presence and abundance of at least such migratory fish as herring and mackerel, and also of the shoals of post-larval young of many of our other food-fishes.

No less than three masses of sea-water of different origin and character may enter or affect the British seas in varying quantity, viz.:—(1) Arctic water such as normally surrounds Iceland and the east of Greenland, and may extend further southwards and eastwards towards Norway, the Faroes, and Shetlands; (2) Atlantic ("Gulf-stream Drift") water which impinges on the western shores of Ireland, and may flood the English Channel and extend round the Shetlands or down into the North Sea; and (3) "Coastal" water such as flows out from the Baltic and, mixed with the other waters, bathes the coasts of N.W. Europe generally, and to a large extent surrounds the British Islands.

The Irish Sea may be regarded as primarily an area of coastal water, which is, however, liable to be periodically invaded to a greater or less extent by bodies of warmer and salter Atlantic water (re-inforced possibly by portions of a deeper outflowing Mediterranean current) carrying in oceanic plankton, and more rarely perhaps by Norwegian or Arctic water causing an invasion of northern organisms. The variations which we find in different years in the nature and amount of the plankton at the same localities no doubt depend to some extent upon the volume and period of such southern or northern invasions; but they may depend also upon other factors, such as the weather (temperature, sunshine, rainfall, wind, etc.) at the time, and previously.

Of the six Copepoda discussed above only one—*Temora*—is a neritic form; the others are all usually regarded as oceanic, that is as having their true home and centre of distribution somewhere to the north, west, or south in the open Atlantic.

The following list gives an approximate indication of what is supposed to be the source of these five oceanic Copepoda:—

Calanus.—N. Atlantic, about Iceland ("Boreal oceanic").
Paracalanus.—Southern, temperate and tropical Atlantic.
Pseudocalanus.—N. Atlantic ("Boreal oceanic").
Oithona.—N. Atlantic ("Boreal oceanic").
Acartia.—N. Atlantic ("Northern styli-plankton").

Some no doubt live on during the year in the Irish Sea, but these indigenous populations are probably reinforced by waves of immigration from outside.

In the case of our Diatoms some of the species of a genus may be neritic and others oceanic, as is shown in the following list, where (N.) stands for neritic and (O.) for oceanic, and a (?) indicates that the evidence seems to me conflicting or inconclusive *:—

Biddulphia mobiliensis (N.), *B. sinensis* (O.).
Coscinodiscus radiatus (O. ?), *C. concinnus* (N.), *C. Grani* (N.).
Lauderia borealis (N.).
Chætoceras boreale (O.), *C. criophilum* (O.), *C. decipiens* (O ?), *C. densum* (O.), *C. contortum* (N.), *C. debile* (N.), *C. diadema* (N.), *C. sociale* (N.), *C. subtile* (N.), *C. teres* (N.).
Thalassiosira gravida (N.), *T. Nordenskioldi* (N.).
Rhizosolenia alata (O.), *R. semispina* (O.), *R. setigera* (N.), *R. Shrubsolei* (N. ?), *R. Stolterfothi* (N. ?).
Guinardia flaccida (N. ?).

It is remarkable how small a number of forms make up the bulk of the macro-plankton throughout the year. These half-dozen kinds of Diatoms and half-dozen Copepoda are the all-important organisms upon which our fate depends so far as concerns food from the sea. That shoals of migratory fish such as herrings and mackerel are attracted in summer and autumn by dense swarms of certain Copepoda such as *Calanus* and *Temora* can no longer be doubted; and there is abundance of evidence that earlier in the year the young stages of other food-fishes, such as plaice, are nourished first by Diatoms and when larger by the smaller Copepoda. These conclusions, however, do not finish the matter. There remains in the sea the much more minute Protozoa and Protophyta of the Nannoplankton, which to a large extent escape through the meshes of our plankton nets and which are doubtless of great importance as the food of Copepoda and other large organisms which in their turn nourish fish.

---

* The matter was discussed more fully some years ago in a paper by Herdman and Riddell in Trans. Biol. Soc. Liverpool, xxv. (1911) p. 178.

There are several other interesting lines of further investigation which open up as collaterals from plankton investigation. One of these is the origin of the great vernal phytoplankton maximum. In the spring there is an awakening of the plant-life of the sea comparable to the growing of the grass and the budding of the trees on land. This cannot be due to any rise in temperature, as the sea at the time that the Diatoms start their active growth and reproduction is at its coldest. We have series of observations extending over more than ten years showing that the water of Port Erin bay is generally of lower temperature in March than in December or January. Of the various causes for the rise in the Diatom curve in these cold waters of early spring I have for some years * regarded with greatest favour the view suggested first by Sir John Murray, viz., the increase in sunlight at that time of year. In that case it would be a photosynthetic phenomenon—the increased solar light energy enabling the Diatoms to obtain from their environment by photosynthesis the materials required for their growth and reproduction. The view that the spring increase in plankton is due to changes in the alkalinity of the water does not in my opinion conflict with the photosynthesis theory but is supplementary to it. The position in regard to the relation between variations in alkalinity and in the plankton, in our district, is as follows:—

The sea around the Isle of Man is a good deal more alkaline in spring (say April) than it is in summer (say July); and during the years 1912–14 Professor Benjamin Moore, by examining samples of sea-water periodically at the Port Erin Biological Station, was able to show † that the alkalinity, which gets low in summer, increases somewhat in autumn, and then decreases rapidly, to disappear during the winter; and then once more, after several months of a minimum, begins to come into evidence again in March and rapidly rises to its maximum in April or May. This periodic change in alkalinity will be seen to correspond roughly with the changes in the living microscopic contents of the sea represented by the phytoplankton annual curve, and the connection between the two will be seen when we realise that the alkalinity of the sea is due to the relative absence of carbon dioxide. In early spring, then, the developing myriads of Diatoms in their metabolic processes gradually use up the store of CO_2 accumulated during the winter and so increase the alkalinity of the water, till the maximum of alkalinity, due to the reduction in amount of carbon dioxide, corresponds with the crest of the phytoplankton curve in, say, April. Prof. Moore has calculated that the annual turn-over in the form of carbon which is used up or converted from the inorganic into an organic form probably amounts to something of the order of 20,000 or 30,000 tons of carbon per cubic mile of sea-water in the Irish Sea; and this probably means a production each season of about two tons of dry organic matter, corresponding to at least ten tons of moist vegetation, per acre—which shows that we are still very far from getting from our seas anything like the amount of possible food-matters that are produced annually.

---

* See "Intensive Study, &c." Part III. p. 260, 1910, Trans. Biol. Soc. Liverpool, xxiv.

† Trans. Biol. Soc. Liverpool, xxix. (1915) p. 233.

Testing the alkalinity of the sea-water may therefore be said to be merely ascertaining and measuring the results of the photosynthetic activity of the great phytoplankton rise in spring due to the daily increase of sunlight.

Other possible causes, more or less related to the above, have been suggested —such as Brandt's hypothesis that the fluctuations in the phytoplankton depend upon the accumulation, and then the exhaustion, of necessary inorganic food-matters in the water, such as nitrogen or phosphorus compounds or silica ; and the view of Nathansohn, Gran and others that vertical currents, carrying up food-matters from the deeper water, have a powerful effect upon the seasonal development of surface plankton. These may be contributory causes or may be effective locally, or on occasions; but it seems probable that a widespread phenomenon of enormous amount such as the vernal increase of phytoplankton must depend upon an equally widespread and powerfully-acting cause such as the rapid increase in the amount of solar light energy which marks the lengthening days of the year in early spring.